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Root diseases and exotic ecosystems : implications for long- term site productivity

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SUMMARY

Root disease fungi, particularly root rotting Basidiomycetes, are key drivers of forest ecosystems. These fungi have co-evolved with their hosts in various forest ecosystems and are in various states of equilibrium with them. Management activities and various land uses have taken place in recent times that have dramatically altered edaphic and environmental conditions under which forest tree species and ecosystems have evolved. For example, in *Sequoia giganteum* stands, fire suppression in this fire dependent ecosystem has resulted in increased mortality due to *Heterobasidion annosum*. On hypothesis is that fire suppression results in increased encroachment of true firs, readily infected by S group *H. annosum*, thereby transferring the disease via root contacts with *S. giganteum*. Also, the existence of a hybrid between the S and P ISG's of *H. annosum* may be evidence for anthropogenic influences on evolutionary pathways in this pathogen. In other ecosystems, such as *Pinus palustris* (longleaf pine) in the southeastern United States, increased mortality following prescribed fire is being observed. Various *Leptographium* species and *H. annosum* have been associated with this mortality following relatively cool temperature fires but how these fungi interact with fire and various edaphic factors are not known. Past agricultural practices that resulted in extensive soil erosion may have given rise to an "exotic ecosystem" in which longleaf pine is now maladapted.

INTRODUCTION

Forest tree species and ecosystems have evolved under stochastic climatic, geological, and biological forces over eons of time. The present flora represents the sum of these selective forces that have acted upon ancestral and modern species. Thus, modern flora is adapted to the conditions existing at present. The stochastic nature of these climatic, geological, and biological selective factors become more striking when considering that possibly 99% of all species that ever existed are now extinct (Raup 1986).

Despite the power of natural phenomena to influence evolutionary pathways, modern man, employing various means in the creation of the infrastructure of civilization, has brought about unprecedented changes and influence upon edaphic and environmental conditions. In many cases, results of these changes are observed by forest pathologists who have an empirical understanding of relationships between site factors, disturbance, past and present management practices, and silvicultural procedures as they relate to many root diseases. These results beg the question as to why, in supposedly co-evolved host-pathogen systems, do we observe excessive mortality and disruption of long-term management goals caused by root disease fungi? The purpose of this paper is to explore, by way of a few examples, the notion of "exotic ecosystems" as a concept that approaches root diseases from a different perspective, one that more directly addresses consequences of management practices.

HETEROBASIDION ANNOSUM AND FIRE

Many forest ecosystems and component tree species have evolved with fire. Some forest types, such as longleaf pine (*Pinus palustris* Mill.) and giant sequoia *(Sequoiadendron giganteum* (Lindl.) Buckholz) depending upon periodic light burns for maintenance of stand vigor and health. The latter tree species was once widely distributed in western North America but is now limited to about 75 groves on the western slope of the Sierra Nevada (Rundel 1972). Until recently, fire suppression over the last 50 or more years in groves of sequoia and mixed conifer forests has resulted in increased fuel loads and an increased component of true firs (*Abies* sp). Because fir stands generally have widespread *Heterobasidion annosum* (Fr.) Bref. infection (Otrosina and Cobb 1989; Otrosina *et al.* 1992, Garbelotto, PH.D. Diss. 1996). contagion towards sequoia roots via contacts with infected firs may be responsible for increased *H. annosum* infection in sequoia. Evidence validating this hypothesis has recently been advanced (Piirto *et al.* 1998). Also, because years of fire suppression result in excessive fuel loads, an unacceptably high risk of infection via fire scars by *H. annosum* and various other pathogenic fungi may exist. Normally, periodic fires that are characteristic of this ecosystem would minimize the true fir component in these stands, thereby reducing the transmission of *H.*

annosum. Nonetheless, fire re-introduction in fire dependent ecosystems must be preceded with caution and understanding of risks involved in this activity.

Another "exotic ecosystem" exemplified by fire exclusion in fire dependent systems is the Sierra east-side ponderosa pine (***Pinus ponderosa*** Doug. ex P. Laws. & C. Laws.) and Jeffrey pine (***Pinus jeffreyi*** E. Murray) type. In many cases, once park-like stands of predominantly ponderosa or jeffrey pines are now dominated by shade tolerant true fir species (Petersen 1989). Since the S biological species of *H. annosum* is widespread on true firs, and apparently infects firs more frequently through natural wounds or means other than cut stumps (Garbelotto *et al.* 1996), characteristically overstocked stands of firs resulting from fire exclusion have a high incidence of root disease that render them susceptible to catastrophic insect outbreaks (Hetert *et al.* 1975) and wildfires (Otrosina and Ferrell 1995). Thus, fire exclusion can be thought of as a disturbance resulting in an "exotic ecosystem" in which current tree species assemblages exist in a pathologically, entomologically, and silviculturally unstable situation that is driven by widespread root disease.

HETEROBASIDION ANNOSUM AND ANTHROPOGENIC INFLUENCES

Heterobasidion annosum S and P biological species in North America have been shown to be genetically distinct entities. Virtually no gene flow occurs between the S and P groups, despite their often close proximity and overlapping host niches (Otrosina *et al.* 1992; Otrosina *et al.* 1993). Recently, a confirmed SP hybrid genet of *H. annosum* was recovered from an east-side Sierra ponderosa pine site in the Modoc National Forest in California (Garbelotto *et al.* 1996). PCR and isozyme analyses confirm that the SP heterokaryon is a true hybrid and is heterozygous for S and P alleles at many loci. Field evidence showed that the SP hybrid genet was extensive in the mortality center and was associated with a slightly symptomatic ponderosa pine and two juniper trees, indicating stability and virulence of the hybrid. An adjacent ponderosa pine stump harbored the hybrid, and may have served as the primary focus of this genet which presumably colonized the roots systems of the adjacent living trees.

The existence of the SP hybrid in *H. annosum* has implications that are relevant to forest management activities as they influence occurrence of this pathogen. Prior to about 200 years ago, forests in the western United States were not harvested extensively and natural processes such as wild fire, insects, and root diseases were in some quasi-equilibrium with insects and with pathogens such as *H. annosum* (Otrosina *et al.* 1992). One question surrounding the existence of the SP hybrid is how, if genetic analyses involving DNA and isozymes provide compelling evidence that gene flow does not occur in nature between the S and P groups, did the hybrid arise given the supposed reproductive barriers (Chase and Ullrich 1990) that exist? One scenario may be the relatively recent advent of timber harvesting during the past 150 years.

Freshly cut stump surfaces are well known to be a suitable niche for the process of infection and colonization. Because stumps of ponderosa pine, other pine species, and true firs can be infected by either S or P group, and because the fungus can survive over 50 years in stumps under western United States environmental conditions (Otrosina and Cobb 1989; Otrosina *et al.* 1992), large numbers of stump infections initiated over the past century can result in increased probabilities that S and P group thalli come into contact. Similar to forced hybridization obtained in laboratory studies (Chase and Ullrich 1990), individual stumps infected by both S and P groups provide suitable opportunities for the hybridization process to occur in nature.

Could the occurrence of the SP hybrid be an indicator of anthropogenic influence on the evolutionary direction in a forest pathogen? The answer awaits further research. Nonetheless, the question has implications for forest management with respect to possible shifts in pathogen host range, transfer of virulence genes, and resultant impacts on forest health.

LONGLEAF PINE, FIRE, AND MORTALITY

Longleaf pine once occupied over 30 million hectares throughout the southern United States (MacCleery, D.W. 1992). At present, only about 5 % of the original longleaf pine sites are currently occupied by this species. Changes in land use such as agriculture, commercial development, and conversion to other forest species such as loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) have contributed to the dramatic decrease in the range of longleaf pine.

Fire is an essential component of the longleaf pine ecosystem, being necessary for the establishment of reproduction and for maintaining stand health. This tree species co-evolved with fire as an essential component of its life cycle. Over the past several years, increased mortality has been observed in certain stands, and this mortality appears to be associated with prescribed burning (Otrosina *et al.* 1995). A preliminary research study conducted at the Savannah River Site, Savannah River Forest Station, in New Ellenton, South Carolina revealed that burned plots had 3 times greater mortality 1 year post burning than unburned check plots. Histological observations on fine roots (< 2 mm in diameter) of longleaf pine obtained from the upper few centimeters of soil in the relatively cool burns have shown internal tissue damage when compared to roots from unburned check plots (Otrosina *et al.* 1995). Stereo microscopic observations of fine roots also reveal evidence of damage present in plots having relatively cool burn temperatures (approximately 80°C at organic matter - soil interface) (Figure 1). Also, 2 to 3-fold differences in isolation frequency of the root pathogens *H. annosum* and *Leptographium* species were associated with roots of mortality trees (Otrosina and Ferrell 1995).

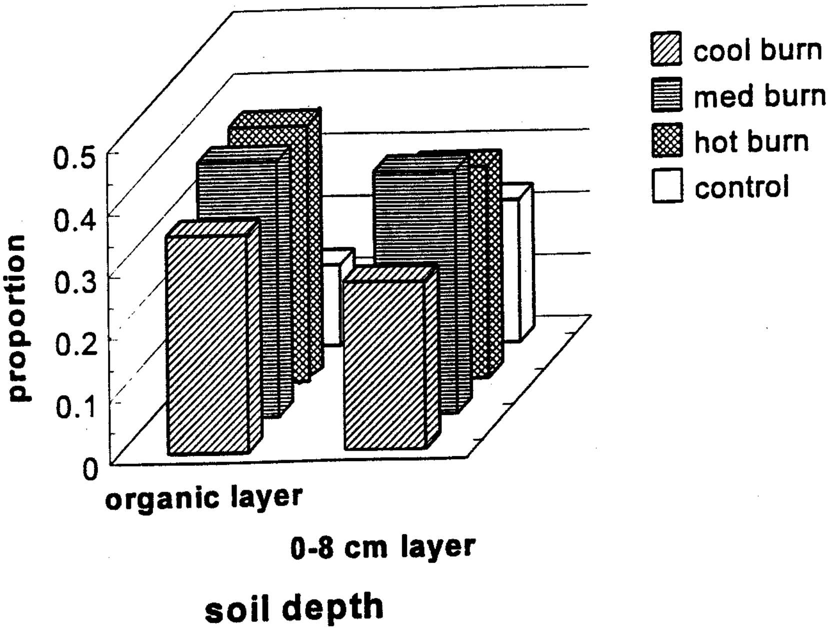

Figure 1. Root damage expressed as proportion of fine root length (<2mm diameter) observed as discolored in 40 year old longleaf pine trees sampled after hot, medium, and cool prescribed burns. Nominal temperatures of the burn plots measured at the soil-organic matter interface were 80°C, 100°C, and 120°C for cool, medium, and hot burn treatments, respectively.

The association of *Leptographium* species with fire and mortality is significant because this fungal genus contains many forest tree root pathogenic species which have varying degrees of pathogenicity toward pine species (Harrington and Cobb 1988; Nevill *et al.*, 1995). Many *Leptographium* species are also associated with various species of root feeding bark beetles which can serve as vectors or as wounding agents that allow introduction of root pathogenic fungi (Harrington and Cobb 1988). Observations of insects in larger woody roots of post fire longleaf pine have been documented (Otrosina *et al.*, 1995) but their roles with respect to these fungi and longleaf pine mortality have not been established.

Regarding these associations with fire, fungi, and insects in longleaf pine, obvious questions arise. Why, in a tree species that is adapted to and has evolved with fire, are we observing root pathogens and associated mortality in such high frequency? What are the roles of these various fungal species and insects in relation to the observed longleaf pine mortality? Longleaf pine has been regarded as either tolerant or resistant to root disease (Hodges 1969) and prescribed fire has been reported to decrease incidence of annosum root disease in southern pines (Froelich *et al.*, 1978).

Observations based upon windthrown trees suggest that on some sites, severe erosion of up to 2 feet of top soil may have severely restricted longleaf pine root systems to the upper 60-70 cm of soil profile (Otrosina unpublished data). Longleaf pine has evolved in deep sands and develops an extensive tap root system in these soils. Thus, although regenerated within physiographically correct sites, longleaf pine on eroded soils are forced into a new ecosystem structure, an "exotic ecosystem", with respect to current soil conditions. These conditions, in turn, may produce unstable and unpredictable outcomes when standard management practices are employed. Precisely what relationships exist between fire, mortality, root disease fungi, and soil conditions form the basis for now ongoing research.

CONCLUSIONS

There are many more examples in forest pathology and entomology where man has unknowingly created certain conditions whereby native organisms, both fungal pathogens and insects, have become serious problems threatening forest sustainability (Goheen and Otrosina 1997; Otrosina and Ferrell 1995). The activities of man have rapidly and dramatically changed landscapes and ecosystems over a short period of time. The adaptations developed over eons of evolutionary time in forest tree species may no longer serve these species when forced into sometimes radically "new" ecosystem structures. These new structures are characterized by interactions not experienced by the tree species in an evolutionary sense, resulting in an unpredictable and unstable or chaotic system (Moir and Mowrer 1995) susceptible to various and unexpected disease problems. The exotic ecosystem concept put forth here views, from a slightly different perspective, subjects contemplated by forest pathologists, entomologists, and silviculturists, encompassing well known abstractions such as predisposing factors, stress, disturbance regimes, and sustainability (Figure 2).

Some viewpoints regarding endemic forest tree root diseases embrace the idea that because these disease causing fungi are endemic to forest ecosystems, they perform beneficial functions among which are creating gaps in forest canopies, decomposing woody debris, or producing cavities for wildlife. These views assert, depending upon management objectives, that root diseases may or may not be detrimental. Such a notion presumes their function and regulatory dynamics are the same at present as they were prior to various management activities. Nevertheless, attention must be granted to the issue that some ecosystems may now be comprised of tree species that are maladapted to current conditions, resulting in varying degrees of instability.

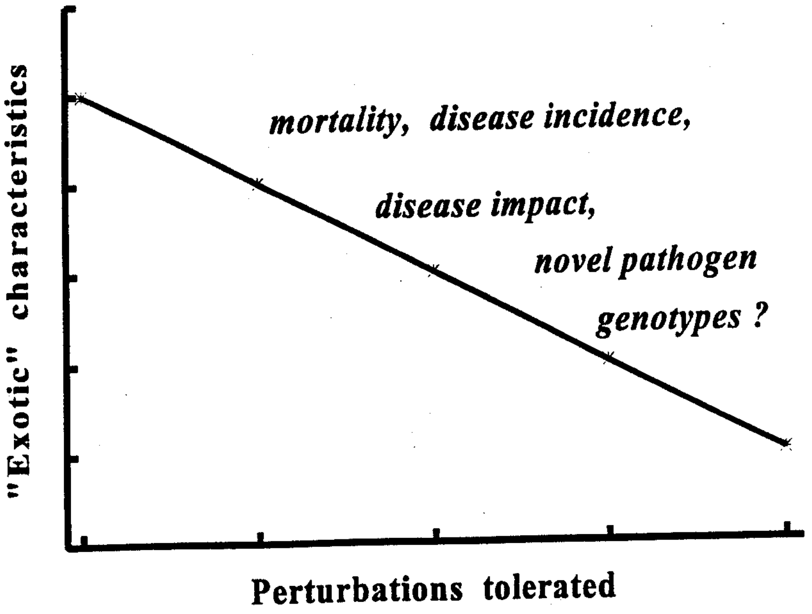

Figure 2. Conceptual model of "exotic" or pathologically unstable ecosystem.

For example, after years of successful wildfire suppression and politically motivated resistance to use of prescribed burning as a silvicultural tool, many forest stands whose natural history involved periodic burning now have large accumulations of litter and fuel. Recent focus on forest health issues acknowledge the importance of fire in many forest ecosystems and are recommending reintroduction of fire to these stands. Forest stands in these situations should be regarded as exotic ecosystems with the appropriate caution exercised. The new set of initial conditions may bring about unexpected forest health problems when fire is reintroduced in many stands. On the other hand, many forest ecosystems are quite resilient and stable under various management regimes, however, it is imperative that we strive to understand disease processes resulting from these new sets of conditions in order to identify which ecosystems and under what conditions do instability and unpredictability develop.

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